Role of Features and Second-order Spatial Relations in Face Discrimination, Face Recognition, and Individual Face Skills: Behavioral and Functional Magnetic Resonance Imaging Data

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Abstract

■ We compared the contribution of featural information and second-order spatial relations (spacing between features) in face processing. A fully factorial design has the same or different "features" (eyes, mouth, and nose) across two successive displays, whereas, orthogonally, the second-order spatial relations between those features were the same or different. The range of such changes matched the possibilities within the population of natural face images. Behaviorally, we found that judging whether two successive faces depicted the same person was dominated by features, although second-order spatial relations also contributed. This influence of spatial relations correlated, for individual subjects, with their skill at recognition of faces (as famous, or as previously exposed) in separate behavioral tests. Using the same repetition design in functional magnetic resonance imaging, we found feature-dependent effects in the lateral occipital and right fusiform regions. In addition, there were spatial relation effects in the bilateral inferior occipital gyrus and right fusiform that correlated with individual differences in (separately measured) behavioral sensitivity to those changes. The results suggest that featural and second-order spatial relation aspects of faces make distinct contributions to behavioral discrimination and recognition, with features contributing most to face discrimination and second-order spatial relational aspects correlating best with recognition skills. Distinct neural responses to these aspects were found with functional magnetic resonance imaging, particularly when individual skills were taken into account for the impact of second-order spatial relations. ■

INTRODUCTION

"Do I know you?" is a phrase that can herald an embarrassing social scenario that many of us have experienced, reflecting a failure to recognize the face of a person we have previously met or the occasional false "recognition" of a stranger. Several lines of evidence indicate that correct recognition of previously seen faces may be a separable process from perceiving certain aspects of the currently seen face (de Gelder & Rouw, 2001; Bruce & Young, 1986; Benton & Van Allen, 1972), both in the normal brain and in neurological cases where one or another aspect of face processing may be selectively damaged (Sergent & Signoret, 1992; De Renzi, Faglioni, Grossi, & Nichelli, 1991; Benton & Van Allen, 1972).

An abundant literature on face processing makes a distinction between part-based or featural information and more holistic or configural processing (Yovel & Duchaine, 2006; Sagiv & Bentin, 2001; Collishaw & Hole, 2000; de Gelder & Rouw, 2000b; Rossion et al., 2000; Tanaka & Sengco, 1997; Tanaka & Farah, 1991, 1993; Sergent, 1984; Carey & Diamond, 1977). Features concern information about the individual parts within a face (e.g., eyes, nose), and are distinct from information concerning relations between such features; the latter which may be divided into several types (Maurer, Le Grand, & Mondloch, 2002). We focus here on the roles of featural information versus second-order spatial relations (i.e., spacing between features). We conducted behavioral studies and related neuroimaging experiments, seeking in particular to exploit any individual differences in face-processing skills and how these might relate to performance in different face tasks and to brain activation under different conditions.

Featural-versus-configural processing for faces has been addressed by many previous studies, including behavioral (Collishaw & Hole, 2000; Tanaka & Farah, 1993; Sergent, 1984; Carey & Diamond, 1977), neuropsychological (Yovel & Duchaine, 2006; Barton, Press, Keenan, & O'Connor, 2002; Moscovitch, Winocur, & Behrmann, 1997), electrophysiological (Sagiv & Bentin, 2001; Eimer, 2000; McCarthy, Puce, Belger, & Allison, 1999; Perrett, Hietanen, Oram, & Benson, 1992), and neuroimaging studies (Yovel & Kanwisher, 2004; Lerner, Hendler, Harel, & Malach, 2001; Rossion et al., 2000). One perspective has emphasized that face processing in general may rely on configural processing, more so for faces than for other

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classes of visual objects (Leder, Candrian, Huber, & Bruce, 2001; Saumier, Arguin, & Lassonde, 2001; Farah, Wilson, Drain, & Tanaka, 1998; Tanaka & Sengco, 1997; Carey, 1992; Levine & Calvanio, 1989). Other authors have emphasized that both featural and configural information may contribute to face processing (Jiang et al., 2006; Yovel & Duchaine, 2006; Collishaw & Hole, 2000; Perrett et al., 1992; Sergent, 1984). This apparently accords with recent functional magnetic resonance imaging (fMRI) studies indicating that featural-versus-configural manipulations of faces may elicit distinct brain responses (Yovel & Kanwisher, 2004; Lerner et al., 2001; Rossion et al., 2000). Those studies contrasted featural and configural processing by manipulating the task (Rossion et al., 2000), the stimuli (i.e., presenting features in canonical or non-canonical face configurations (Lerner et al., 2001), or both task and stimuli (Yovel & Kanwisher, 2004). However, the precise anatomical localization of putative featural-versus-configural face processing, as indicated by fMRI, appears somewhat inconsistent across existing studies. Featural processes have been attributed to the bilateral lateral occipital cortices (LOC, Yovel & Kanwisher, 2004; Lerner et al., 2001) or to the left fusiform face area (FFA, Rossion et al., 2000), while configural processing has been attributed to the bilateral fusiform gyrus (FFG, Lerner et al., 2001), to the right FFA alone (Rossion et al., 2000), or to neither (Yovel & Kanwisher, 2004).

The operational definitions of featural-versus-configural processing often varied between such studies (e.g., configural corresponded to holistic in Rossion et al., 2000; to first-order relations in Lerner et al., 2001; to second-order spatial relations in Yovel & Kanwisher, 2004) or were not always clearly stated (cf. Maurer et al., 2002). This might account for some of the differences in fMRI outcome. Here, we defined featural-versus-configural processing in terms highlighted by the overview of Maurer et al. (2002). The eyes, nose, and mouth were considered to provide facial ''features,'' while the second-order spatial relations between these (i.e., spacing of the eyes, nose, and mouth relative to each other and to a constant face outline) provided the ''configural'' cues for our stimulus manipulations (see also Yovel & Kanwisher, 2004). Note that although there may also be other aspects of processing that might be considered configural, such as first-order relations or potentially holistic properties (see Maurer et al., 2002), we focused solely on second-order spatial relations, both for operational clarity and because these aspects are thought to be particularly important for face individuation and recognition (Sergent, 1984). Notably, this was commented upon long ago by Carl Lewis (1865), in the dialog between Humpty Dumpty and Alice, and has also been emphasized in much recent empirical work (e.g., Rhodes, Carey, Byatt, & Proffitt, 1998; Carey, 1992; Sergent, 1984).

The roles of featural and second-order spatial relation information in faces are commonly tested by assessing participants' ability to detect changes in either of these two aspects (when changing facial features or changing the spatial location of otherwise comparable features within a face; e.g., Yovel & Duchaine, 2006; Yovel & Kanwisher, 2004; Barton et al., 2002; Maurer et al., 2002; Le Grand, Mondloch, Maurer, & Brent, 2001). This raises the question of whether, or indeed how, to ''equate'' such changes for comparison. In some studies, featural and second-order spatial relation changes have been putatively equated by carefully matching these changes for overall behavioral difficulty in normal observers (e.g., see Yovel & Kanwisher, 2004; Le Grand et al., 2001). Although this approach can be experimentally elegant, it runs the potential risk of producing unnatural stimuli that may not reflect the usual roles or relative weights of featural-versus-second-order spatial relation information within real faces. For instance, if features normally differ more between distinct real faces than second-order spatial relations, then the latter cues might have to be ''exaggerated'' to match for difficulty, which could then lead to overestimates of their usual weight, or vice versa. Accordingly, the approach we took here was to utilize the natural range of featural and spatial relation differences, as observed in original (real) face photos.

Previous studies that equated difficulty for normal participants have suggested that prosopagnosic patients are more impaired in detecting changes in second-order spatial relations than in features of faces (Barton, Cherkasova, Press, Intriligator, & O'Connor, 2003; Barton et al., 2002), although featural process may be also impaired in some of these patients (Yovel & Duchaine, 2006). This accords with the common idea in the face literature that spatial relations in faces may be particularly critical for face recognition. Surprisingly, however, a recent fMRI study (Yovel & Kanwisher, 2004) did not observe increased responses for second-order spatial relation processing in faces in the ventral visual FFA. In that study, participants performed a one-back repetition detection task, focusing either on the features or second-order spatial relation aspects of faces, with the experiment seeking to match these two tasks for discrimination difficulty. The study reported an increase in response in ''object-selective regions'' (LOC, which includes the lateral and ventral occipital cortex) when attending to features compared with when attending to spatial relation aspects (Yovel & Kanwisher, 2004). Note that this type of design, as in several previous fMRI studies, also typically tests for featural or spatial relation processing by contrasting them directly against each other (Yovel & Kanwisher, 2004; Lerner et al., 2001; Rossion et al., 2000). In such a design, any regions that may process both types of information in faces cannot readily be detected. In the present fMRI study, we used a paradigm that allowed us to test for featural and second-order spatial relation processing independently, in a fully factorial 2×2 design.

We used a combination of behavioral and fMRI experiments. As noted above, one key aspect of our studies was that we allowed the featural and second-order spatial relation cues to vary over the ''natural range'' from the set of real face photos that we manipulated. Although this may not equate the resulting stimuli for experimental ''difficulty'' (cf. Yovel & Kanwisher, 2004; Le Grand et al., 2001), it may accord better with actual variation among natural faces. We then measured the impact of featural and second-order spatial relation information on each participant in a person-discrimination task (''Do two successive face images show the same or a different person?''), rather than equating this contribution experimentally. We also sought to take advantage of any individual differences in the contribution of the different types of information (thus, any variation in face-processing skills) that may arise spontaneously in the group of neurologically intact individuals whom we studied.

We used an immediate pair repetition paradigm (cf. Rotshtein, Henson, Treves, Driver, & Dolan, 2005; Eger, Schyns, & Kleinschmidt, 2004; Winston, Henson, Fine-Goulden, & Dolan, 2004), manipulating whether all face features were the same or different, and independently whether the second-order spatial relations between features were same or different, in a fully orthogonal 2 × 2 design (Figure 1A). In a behavioral context, participants judged whether two successive faces in a pair represented the same or a different person (person individuation, or equivalently person-discrimination task).

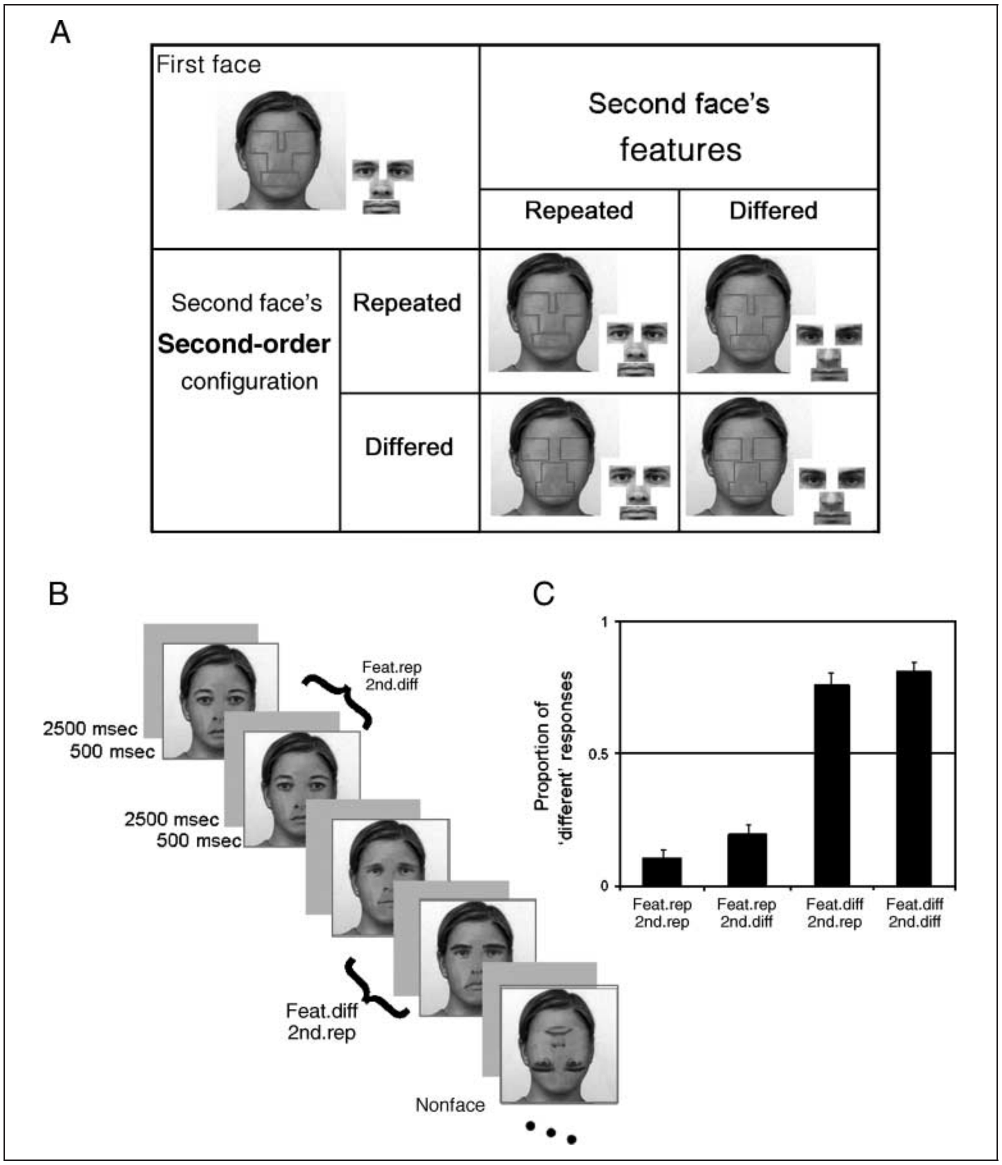

Figure 1. Person-discrimination experiment. (A) The 2 × 2 design had two orthogonal factors: feature change/repeat and second-order spatial relations change/repeat. Within a pair of faces, the second stimulus either repeated or differed from the first stimulus in its component features (eyes, nose, and mouth) and/or independently in the spatial layout of these component features. At upper left is an example of the visual elements used to generate a first face in a pair. The four cells in the 2 × 2 ''table'' display examples of the possible second faces that could follow. The ''raw materials'' that generated each stimulus are shown: the blank face with sex-nonspecific haircut and outer features served as the template, whereas the lines mark where each feature was located; on the right of each face are shown the four rectangles containing the featural information. The spatial locations for placing these features onto the template define the second-order configural spatial relations. Upper row for same second-order spatial relations (i.e., configural spacing) as in first face; bottom row for a different second-order spatial relations (taken from a different face in the original unmanipulated photos). (B) Example sequence of stimuli as they appeared in the experiment. This sequence represents the fMRI experiment, in which a continuous stream of stimuli was presented and participants made a face/nonface decision. Note that the pair structure depicted in (A) was, thereby, concealed within the ongoing stream, by random interleaving of conditions, and inclusion of filler ''nonface'' stimuli. (C) Results of Experiment 1, the person-discrimination experiment. The proportions of ''different'' responses for the different types of pairs are presented, along with standard error of the mean. 2nd.diff = changes of second-order relations; 2nd.rep = repetition of second-order relations; Feat = feature.

In this way, we measured the impact of changing features and/or changing second-order spatial relations on person-discrimination judgments, plus any individual differences in the impact of features or of second-order spatial relations upon this. We could, thereby, assess the relative contribution of each of these two cues to face processing when varying these over the ranges found in the natural set of faces used, for each participant.

We found that featural changes had a stronger influence than second-order spatial relations cues on person discrimination but that second-order spatial relations cues also contribute. The relative impact of each cue type on person discrimination varied from one participant to another. Having thus indexed any individual differences among our neurologically intact participants, in the impact of features or second-order spatial relations on person discrimination, we next tested whether these individual differences correlated with performance on other face-processing tasks. Specifically, we conducted three entirely separate tests of face recognition. One tested for delayed explicit recognition after incidental exposure to previously unknown faces. The second tested for explicit recognition of famous faces. In both these cases, we implemented objective signal detection measures of face-recognition skill. The third measure was a subjective self-rating of face recognition. Remarkably, we found that individual differences in objective and subjective face recognition, measured on these separate tests, correlated with the impact of second-order spatial relations cues, as measured in the separate person-discrimination task for each individual participant.

In an fMRI experiment, we used a similar immediate repetition/nonrepetition design as in the behavioral person-discrimination task but now using a separate set of naive subjects and without imposing explicit person discrimination during scanning (to avoid possible contamination of fMRI results by behavioral performance and potential differences in ''difficulty''). Our fMRI data showed that featural changes (vs. repetition) influenced the response of lateral occipital sulcus (LOS) and the right FFG. Second-order spatial relation changes had a distinct neural impact on the inferior occipital gyrus (IOG) and also on the right FFG, but this was revealed only by considering individual differences in the impact of these changes, as measured in the separate behavioral person-discrimination task.

EXPERIMENT 1: PERSON-DISCRIMINATION TASK

Methods

Participants

Nineteen healthy volunteers (9 women and 10 men; mean age = 25 years, range = 18–35) participated in behavioral experiments (Experiments 1 and 2; see next section for the latter). One participant failed to use the correct response buttons during the person-discrimination task and was thus excluded from analysis. Participants had normal or corrected visual acuity, and no current or past neurological or psychiatric history. Informed consent was obtained in accord with the local ethics committee.

Stimuli

The initial stimulus set comprised 30 achromatic front-view faces with neutral expressions, taken from the Karolinska Directed Emotional Faces set (KDEF; Lundqvist & Litton, 1998). The stimuli were created using PhotoShop 6.0 (Adobe, CA). We first overlaid on each face an identical outer contour that ensured faces only differed in their inner features. This outer-contour frame was created by combining outer features (hair, ears, neck, etc.) from different faces of the same original KDEF set and had a unisex appearance that was identical across all faces (see examples in Figure 1). Four virtual rectangles (identical in size across faces) were manually placed on each face, two around the eyes (bordering the nose bridge and the eye brow), one around the nose (aligned with the starting point of the ''valley'' between the nose and the cheek), and one around the mouth (bordering the chin; see Figure 1). The content of these rectangles was operationally defined as providing the facial features, whereas the spatial arrangement of these rectangles defined the second-order spatial relation manipulation.

A blank face with skin texture and a constant outer-contour frame (see above) served as the template image (see Figure 1A). The feature rectangles were overlaid onto this template image to generate each new face stimulus. The spatial relations between the feature rectangles could match the spatial relations within the original face for those features or instead match the spatial relations from a different face from the original natural set (see Figure 1A). Examples of the final stimuli used are presented in Figure 1B. Three judges in a pilot study could not reliably distinguish between natural faces with features and second-order spatial relations from the same person and from two different persons. Importantly, our second-order spatial relations and featural manipulations were based on variation of these parameters within the face set we used (i.e., total of 30 faces), using the values found naturally within the original set.

To provide an estimate of the extent of the second-order spatial variation within the set of faces (disregarding local feature changes), we measured this variation among five landmark points within each face: right and left pupils, tip of the nose, upper lip at the extremity of the ''Cupid's bow,'' left earlobe, and the midpoint of the hairline. Note that the locations of the last two landmarks were fixed across subjects and, therefore, provide an objective measure of absolute differences between faces. We first calculated the Euclidean distances between each of these landmarks and the left eye. Then, we measured the differences in these distances between the face pairs from the experiment (see Procedure) for equivalent features. These difference scores were converted to percent change by dividing them with the fixed distance between the two earlobes (which was part of the outer-contour template and, hence, constant across all faces, see above). The percent change provides a metric of physical change between pairs of faces in spatial relations. Mean variations in second-order spatial relations between the two pupils were 2.5 ± 1.8% (*SD*); the left pupil and the tip of the nose, 1.8 ± 1.8%; the left pupil and the upper lip, 1.9 ± 1.5%; left pupil and left earlobe, 2.3 ± 1.7%; left pupil and hairline, 2.27 ± 0.63%. In terms of viewing angle during the behavioral session, these changes were all less than 1°. The mean second-order spatial relation changes between pairs of faces, sum up to 13.8% of the face width (i.e., distance between the two earlobes).

Procedure

We used an immediate pair repetition paradigm, manipulating change or repetition across successive pairs of stimuli in a factorial 2 × 2 design, with the orthogonal factors of feature change (different or repeat) and second-order spatial relation change (different or repeat). Thus, within each successive pair of faces, features or their second-order spatial relations could repeat or differ, independently (Figure 1A). Each condition included 15 different face pairs. Each pair was presented twice (giving a total of 30 pairs per condition). Stimuli size was 7.2 cm^2 and view angle was approximately 4.12°. A pair trial started with an empty circle presented for 500 msec that cued the participant to get ready. Each face in a pair was then presented for 500 msec, with a 500-msec interval between them, and the trial ended with a 2000-msec fixation point or after participants responded. Participants were instructed to judge whether the two successive faces appeared to depict the same person or two different persons. The task of person-discrimination was described in this subjective way and with reference to people rather than images, with the aim of approximating natural face individuation processes, rather than assessing the ability to detect any visual changes whatsoever between two successive retinal images. Participants were asked to respond as quickly and accurately as possible. Stimuli were presented, and responses were collected using Cogent2000 software (www.vislab.ucl.ac.uk/Cogent/index.html).

Data Analysis

Data were analyzed using Matlab 6.0 (The MathWorks) and SPSS 13.0. Results for the subjective person-discrimination task are presented (Figure 1C) as the proportion of ''different'' responses in the total number of pairs per condition (i.e., out of 30). For each participant, we estimated the impact of a given type of change by subtracting the proportion of ''different'' responses for the repetition trials from those for the nonrepetition trials for each dimension separately. Thus, for example, the impact of changing the features on person discrimination was defined as featural different minus featural repeat (for proportions of ''different'' responses). Note that this measure was based on subjective judgments by participants that pairs of faces depicted the same person or two different people, rather than a strictly objective measure of whether there had been any image change whatsoever. We chose this subjective measure because we were interested in investigating the conditions that affect the individuation process (i.e., what leads participants to decide that two faces depict two different individuals). As will be shown, this measure proved to be very revealing, correlating both with other more objective behavioral indices in separate experiments and also with some of the later fMRI results. Correlation between the impact of feature and second-order spatial relations changes were tested using nonparametric Spearman's ρ and significance was tested using two-tailed Student's t distribution with $n - 2 = 16$ degrees of freedom.

Results

We assessed the influence of the different conditions on the proportion of ''different'' judgments in person discrimination, using repeated measures analysis of variance with two factors (featural change or repeat and second-order spatial relations changed or repeated). We found that judgments were strongly affected by featural changes compared with featural repeats [$F(1,17) = 407$, $p < .001$; see Figure 1C]. Performance was also significantly affected by changes of second-order spatial relations [$F(1,17) = 19.9$, $p < .001$], although less so. The interaction did not reach full significance [$F(1,17) = 2.55$, $p = .1$]. The impact of featural changes (increased proportion of ''different'' responses being 0.65 ± 0.14 when features changed versus remained the same) was much larger than the corresponding impact of second-order spatial relation changes [0.084 ± 0.08; $t(17) = 16.8$, $p < .001$]. Thus, featural changes had more impact overall in the present on-line person-discrimination task, although second-order spatial relations also had some influence. There were no significant differences in reaction times between conditions (all ps > .1).

We next tested whether the results were consistent across stimulus pairs, reanalyzing the data now using pairs as the random term with 15 levels (1 for each particular pair). For each condition, we calculated a χ^2 statistic that tested whether some pairs tended to be judged significantly more frequently as ''different'' (or ''same'') than others. There were no significant differences between pairs [all $\chi^2(14) < 23$, ps > .05].

As a first approach to possible individual differences, we tested whether the overall impact of featural change on particular participants' judgments correlated with the overall impact of second-order spatial relations changes. No such relations were found [Spearman's $\rho = 0.23$, $t(16) = 0.94$, $p = .4$]. Although this lack of correlation could, in principle, reflect a lack of power, we think this is unlikely, because clear correlations with other behavioral measures were found for the present group of subjects (see below). Instead, we suggest that the lack of correlation might arise because detection of featural changes and of second-order spatial relations changes in faces may reflect some separate skills and distinct neural processes, as further elaborated on below, and ultimately confirmed here with fMRI.

The greater impact of featural than spatial relation changes overall in Experiment 1 (see Figure 1C) at first glance seems in apparent conflict with a common emphasis in the face literature on a critical role for second-order spatial relations (and for configural processing more generally). For instance, it has been suggested that deficits in prosopagnosia may particularly implicate second-order configural spatial relations, rather than processing of facial features (Barton et al., 2002). But note that prosopagnosia commonly presents as a failure to recognize faces rather than to discriminate or individuate them per se (Benton & Van Allen, 1972). Our next behavioral experiments sought to determine whether individual differences among our group of neurologically intact individuals, in the impact of second-order spatial relations, might be related to individual variation in their abilities at recognizing faces, more so than for the impact of features.

EXPERIMENT 2: MEASURES OF PARTICIPANTS' FACE-RECOGNITION SKILLS

The ability to recognize faces was assessed by three independent behavioral measurements, implemented separately from Experiment 1 and using entirely different stimuli. Two of the new tests (Experiments 2a and 2b) provided objective measures of face recognition, whereas a third (Experiment 2c) comprised a subjective self-evaluation of face-recognition skill in daily life. We related each of the measures from Experiments 2a, 2b, and 2c to the separately obtained data for the same participants from the person-discrimination task in Experiment 1, which had indexed the impact of featural changes and of second-order spatial relational changes on person discrimination for each of these participants.

Methods

Participants were identical with those from Experiment 1 (see above).

Experiment 2a: Incidental Learning of Newly Exposed Faces

Stimuli

Forty faces with different identities (20 women and 20 men) were taken from the KDEF set (Lundqvist & Litton, 1998). Note that the faces used in this experiment had different identities from those used in the person-discrimination experiment (Experiment 1), with no overlap in stimuli. Experiment 2a had two phases, an incidental study phase, followed approximately 45 min later by a recognition test phase. In the study phase, we used colored close-ups of happy facial expressions in three different view points (frontal, left three quarter, and right three quarter; Figure 2A). For the test phase, images of the same identities were used but now zoomed to an extreme close-up frontal view, achromatic, and with neutral expressions rather than happy (Figure 2B). This was done to ensure that recognition should not be based on low-level properties of the visual image but rather on encoding of individual face properties.

Experimental Procedure

The incidental study phase occurred at the beginning of the experimental session (before Experiment 1). In this phase, we used a likeability rating task. Participants were presented with three different views of the same face with a happy expression for 5 sec and instructed to study the faces closely. After the faces disappeared, they were prompted with a question that asked them to state how much they liked this person on a scale from 1 to 6, with 1 being ''I don't like this person at all'' and 6 being ''I like this person very much and would be happy to meet him/her''. The next identity appeared after participants gave their rating. Twenty identities (10 women) counterbalanced across participants were chosen randomly for the study phase from the total 40 identities. The incidental learning procedure and likeability rating were chosen as we sought to approximate real-life encounters and to accord with the Warrington face-recognition procedure (Warrington & James, 1967), which uses a similar exposure task during their incidental learning procedure. In between the initial incidental study phase and the later recognition test, subjects participated in other face-related tasks (in the following order: person discrimination, Experiment 1; recognition of famous faces, Experiment 2b, and other face-related experiments that are not reported here) but with no overlap in the stimuli used (with Experiment 2a). Altogether, more than 250 photographs of faces (all with different identities) intervened, with a mean time separation of approximately 45 min between the incidental study phase and the test phase.

In the recognition test phase, participants performed a familiarity judgment on 40 identities (of which 20 had been presented in the earlier study phase and 20 new identities). Faces were presented in random order for 750 msec each, with an intertrial interval up to 2000 msec (depending on response time). Participants were explicitly instructed that these faces might have identities that had appeared earlier, and if so, the face would always be a different image of that person. They were instructed to

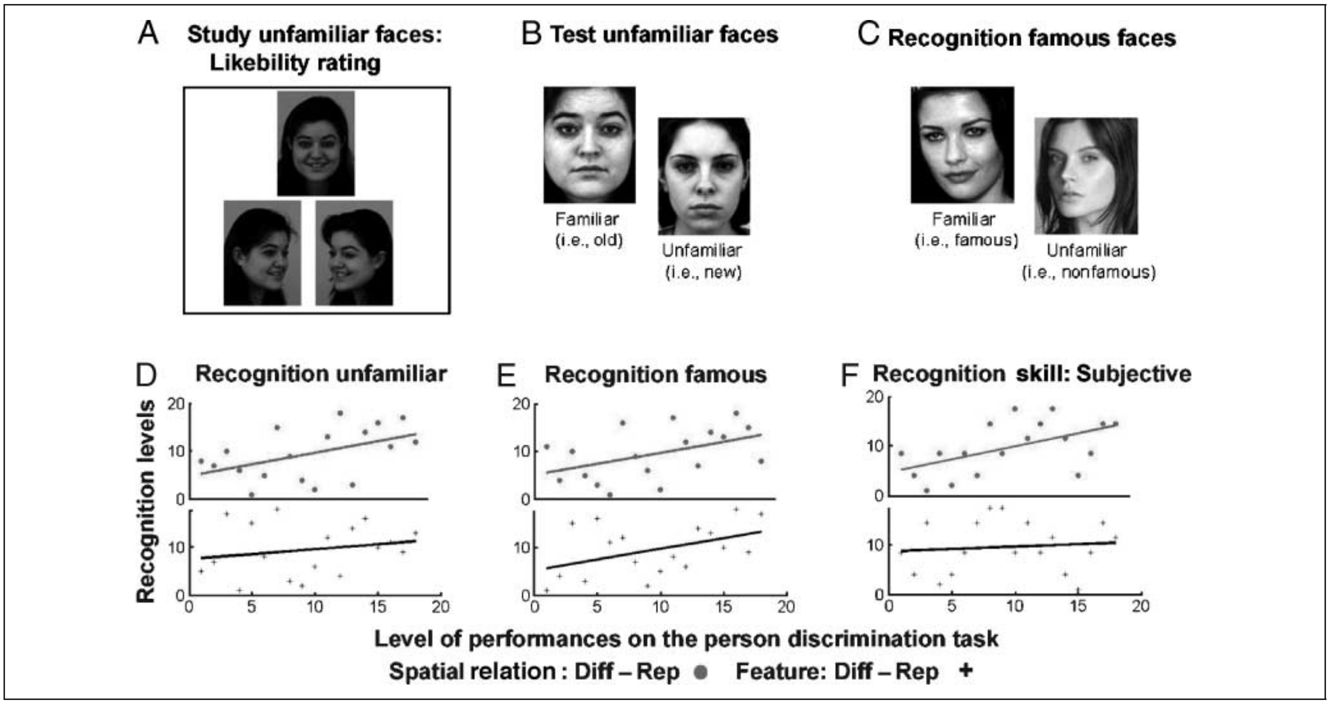

Figure 2. Face recognition measurements. Examples of stimuli used for the face recognition tests. Two objective measures of face recognition ability were used: incidental learning of newly exposed faces (Experiment 2a) and recognition of famous faces (Experiment 2b). (A) Example of the stimuli used in the study phase of the incidental learning task (Experiment 2a). Three different viewpoints of the same individual with a happy facial expression were presented simultaneously for 5-sec. Participants were asked to rate the likeability of each individual. (B) In the test phase, of Experiment 2a, achromatic zoomed close-ups of the 20 individuals presented in the study phase were randomly interleaved with 20 new individuals. All faces had neutral expressions. Participants were asked to make a yes/no recognition judgment on each face, presented singly. (C) Examples of stimuli that were used in the famous face recognition test. Note that the face images were chosen with care such that famous and nonfamous faces should not differ in their compositions. (D–F) Scatterplots of individual participants' behavioral impact of featural changes on proportion of "different-person" responses (black crosses, bottom) and likewise for the impact of second-order relational changes (circles, top), plotted against the three measures of face recognition: (D) Experiment 2a, d' of the incidental learning; (E) Experiment 2b, d' of the recognition of famous faces; (F) Experiment 2c, subjective rating of face recognition. Note that the scatterplots describe the nonparametric correlations used, thus, the values are rank orderings of the original values for each behavioral measure. The impact of second-order spatial relations (circle, top) correlated with all three measures of face recognition (all ps $< .05$), whereas the impact of featural change (black crosses, bottom) correlated only with recognition of famous faces Experiment 2b ($p < .05$). See main text of Results for more details.

work with their gut feeling of familiarity. Foil (new) and target (old, previously exposed during study phase) were fully counterbalanced across participants.

Data Analysis

Data were analyzed using signal detection theory. For each participant, d' for sensitivity to previously seen faces and a decision criterion (β) or response bias were estimated (Snodgrass & Corwin, 1988). Correct recognition of a previously seen face constituted a hit, whereas erroneously recognizing a novel face as familiar constituted a false alarm. Hit and false alarm rates were transformed to Z scores using the standard normalized probability distribution. The d' values were estimated as the difference between the standardized scores (Z) of the hit rates (H) and of the false alarm rates (FA)

$$d' = Z_{\mathrm{H}} - Z_{\mathrm{FA}}$$

Decision criteria (β) was estimated as the ratio of the densities of the hit and the false alarm rates, again transformed using the standard normalized probability distribution and calculated as

$$\beta = f_0(Z_{\mathrm{H}})/f_{\mathrm{n}}(Z_{\mathrm{FA}})$$

where f_0 is the height of the normal distribution over Z_{H}, and f_{n} is the height of the normal distribution over Z_{FA} (Snodgrass & Corwin, 1988).

Correlations between behavioral measures (e.g., those from Experiments 1, 2a, 2b, and 2c) were calculated using nonparametric Spearman's ρ correlations in SPSS 14.0, with each participant contributing one score per behavioral measure. We used a nonparametric test (i.e., Spearman's ρ) for subject-by-subject correlations between different behavioral measurements to ensure that our results were not unduly influenced by outlier participants. Significance was tested with a one-tailed t distribution with $n - 2 =$

16 degrees of freedom, as any increase in sensitivity to a particular facial property (i.e., impact of featural changes, particularly, of second-order spatial relation changes, in Experiment 1) was expected to correlate positively with any estimates of face-recognition skill (in Experiment 2). Two participants did not make any false alarms in Experiment 2a, precluding a reliable estimation of their decision criterion (β) and, hence, were omitted from correlation tests that involved the β criterion.

Experiment 2b: Recognition of Famous Faces

Stimuli

One hundred fourteen achromatic close-ups of famous people and 114 achromatic close-ups of unfamiliar faces were used. An effort was made to match the photo composition of the unfamiliar faces to that of the famous faces by using photos taken from unknown models' books and of politicians from distant regions (Figure 2C). This was done to ensure that recognition of famous faces could not be performed based on cues in the photo composition but rather on familiarity with individual face properties. In a pilot study, two judges confirmed the anonymity of the unfamiliar faces and the familiarity of the famous faces in the context of young (20–40 years) London/British culture.

Experimental Procedure

Stimuli were presented in random order, each for 750 msec with an interstimulus interval of 750–2000 msec (depending on participant response time). Participants performed a yes/no familiarity judgment on the faces. They were explicitly instructed to work with their gut feeling of familiarity, rather than rely on any semantic contextual cues. They were also explicitly instructed that the photos of the unfamiliar faces might have a similar photo composition to the photos of the famous individuals, so they should not base their judgment on photo composition. Experiment 2b was run after the study phase of Experiment 2a and after Experiment 1.

Data Analysis

Data were analyzed using signal detection theory and then nonparametric correlations (i.e., Spearman's ρ) with the other behavioral measures, similar to Experiment 2a. Hits comprised correct recognition of famous faces, whereas incorrectly recognizing an unfamiliar face as familiar counted as a false alarm.

Experiment 2c: Subjective Self-ratings of Face-recognition Skill in Daily Life

Participants were requested to rate their face-recognition skill in daily life on a scale of 1 to 10 at the beginning of the experimental session (before performing the study phase of Experiment 2a), with 1 being ''I cannot remember faces at all'' and 10 being ''I never forget a person's face once I met him or her.'' Subjects were explicitly instructed that this rating was not about their naming skills or their ability to retrieve semantic information regarding individuals but just about their ability to recognize faces in daily life. Correlation with the other behavioral measures (Experiments 1, 2a, and 2b) were calculated using nonparametric Spearman's ρ, and significance was tested with a one-tailed t distribution.

Results

First, to test for any relations between the three recognition skill measures, we computed correlation analyses on individual scores in Experiments 2a, 2b, and 2c. The two independent objective measures of face-recognition skill (Experiments 2a and 2b) were highly correlated. The d' and response bias values estimated from recognition of exposed but previously unknown faces (incidental learning, Experiment 2a) were highly correlated with those estimated separately from the recognition of famous faces in Experiment 2b [d': Spearman's $\rho = 0.795$, $t(16) = 5.24$, $p < .001$; β: Spearman's $\rho = 0.794$, $t(16) = 5.22$, $p < .001$]. This suggests that some related mechanisms may underlie recognition of recently seen but previously unfamiliar faces and of famous faces. This result is in agreement with other recent work (Goshen-Gottstein & Ganel, 2000). On the other hand, the subjective measure of face-recognition skill (Experiment 2c) did not correlate with the d' objective measures of that skill (Experiments 2a and 2b) [all Spearman's $\rho < 0.03$, $t(16) < 0.12$, $p > .1$]. This suggests that objective measures may tap into different aspects of face-recognition skill than subjective self-ratings.

More importantly, the impact of second-order spatial relations on person-discrimination judgments (as measured in Experiment 1 for each individual), correlated with all three separate measures of face-recognition skill (Figure 2D–F). The impact of second-order spatial relation changes in Experiment 1 for individual participants correlated with their d' for incidental face-recognition in the entirely separate task of Experiment 2a [Spearman's $\rho = 0.45$, $t(16) = 2.01$, $p < .05$] and with their d' for recognizing famous faces in Experiment 2b [Spearman's $\rho = 0.436$, $t(16) = 1.94$, $p < .05$). Thus, the impact of second-order spatial relational changes (in unknown faces that do not have to be remembered) in Experiment 1 was positively related to individuals' abilities to recognize newly learned faces (after a delay of ~45 min) and to recognize famous faces. It did not correlate with the response bias measures for either of the objective recognition tasks (all $p > .1$). Finally, the impact of second-order spatial relational changes on particular participants in the person-discrimination task also correlated with their self-ratings of face-recognition ability in daily life [Spearman's $\rho = 0.54$, $t(16) = 2.56$, $p < .01$]. Thus, remarkably more than 20% of the variability between participants in their face-recognition skills can be explained by the impact of second-order spatial relations on their person discrimination.

By contrast, individual differences in the impact of featural changes for the person-discrimination task of Experiment 1 neither correlated with the incidental learning task in Experiment 2a [Spearman's $\rho = 0.2$, $t(16) = 0.8$, $p = .2$] nor with self-rating of recognition skill [Experiment 2c: Spearman's $\rho = 0.12$, $t(16) = 0.48$, $p = .3$]. There was, however, some correlation with recognition of famous faces [Experiment 2b: Spearman's $\rho = 0.44$, $t(16) = 1.96$, $p < .05$], indicating that features might perhaps become important for recognizing overlearned faces. As with spatial relations, the impact of featural changes did not correlate with response bias measures for any recognition tests (all $p > .1$). The absence of correlations between impact of featural changes and the other recognition measures seems unlikely to merely reflect restriction of range on the individual feature scores, because variability on the impact scores was actually more widely spread for features (ranging from 0.36 to 0.83 of proportional change in ''different'' responses when features changed, with $SD = 0.18$) than for the impact of second-order spatial relations changes (ranging from −0.01 to 0.25, with $SD = 0.08$).

EXPERIMENT 3: FUNCTIONAL MAGNETIC RESONANCE IMAGING EXPERIMENT

The preceding behavioral experiments showed that features had a greater overall impact on person discrimination than second-order spatial relations, although the latter did have some impact (Experiment 1). Moreover, individual differences in the impact of second-order spatial relations (Experiment 1) related to individual differences in objective and subjective aspects of face recognition (Experiment 2). We next sought to test with fMRI for brain activations due to changes of features or to changes of second-order spatial relations and more particularly (given the results of Experiment 2) any fMRI effects related to individual differences in the impact of second-order spatial relations. Most previous fMRI studies of featural-versus-spatial relation processing of faces have not considered individual differences among neurologically intact participants (but see Gauthier, Tarr, Anderson, Skudlarski, & Gore, 1999, who manipulated training, rather than looking at spontaneous individual differences, as in this study and did not focus on featural and spatial relation processing, unlike here).

The design used for our fMRI study ($n = 14$) was analogous to the design for Experiment 1. We again manipulated whether operationally defined face features changed or not and orthogonally whether second-order spatial relations changed or not across two successive face stimuli. This was implemented in a fully factorial 2 × 2 immediate repetition design. In this way, we could test for any repetition effects on fMRI (cf. Grill-Spector, Henson, & Martin, 2006; Rotshtein et al., 2005; Eger, Henson, Driver, & Dolan, 2004; Winston et al., 2004; Henson & Rugg, 2003; Avidan, Hasson, Hendler, Zohary, & Malach, 2002; Henson, Shallice, & Dolan, 2000; Kourtzi & Kanwisher, 2000) related to either repeated features or second-order spatial relations. Importantly, the factorial design enabled us to test effects of featural and second-order spatial relation changes independently and thus to delineate any regions that may be sensitive to only one type of information or both types. This design differs from other recent fMRI studies testing featural-versus-more configural processing where typically the two putative processes were compared with each other directly (e.g., Yovel & Kanwisher, 2004; Rossion et al., 2000) rather than orthogonally as here.

A further key aspect of our fMRI study was consideration of individual differences in the impact of second-order spatial relations (or featural information) as separately assessed behaviorally. The behavioral measures were implemented after scanning, using an analogous behavioral person-discrimination task as in Experiment 1, plus subjective rating of recognition skill as in Experiment 2c.

Methods

Participants

Fourteen healthy volunteers participated in the fMRI experiment (9 women and 5 men; mean age = 29 years, range = 19–51). All participants had normal or corrected visual acuity and no concurrent or past neurological or psychiatric history. Informed consent was obtained in accord with local ethics.

Experimental Procedure

An immediate pair repetition paradigm was used (see also Rotshtein et al., 2005; Winston et al., 2004; Kourtzi & Kanwisher, 2000), with four types of successive pair being possible among an ongoing stream of stimuli. An identical set of stimuli was used as in Experiment 1, although the image size (here, 12.6 cm^2) and view angle (here, 3.4°) of stimuli differed, but the second-order spatial relations changes remained, on average, less than 1° of visual angle. The 2 × 2 design was analogous to that used in the person-discrimination behavioral experiment (Experiment 1), with one factor of featural change or repetition, and a second orthogonal factor of second-order spatial relation change or repetition (Figure 1A). For efficiency (and to ''disguise'' the pair repetition structure of the fMRI experiment and, thereby, minimize attention and strategic confounds), faces were now presented in a continuous stream, with each face appearing for 500 msec, separated by an interstimulus interval of 2500 msec containing only a central fixation point (Figure 1B). Half of the stimuli were nonfaces. These were generated by inverting the inner feature rectangles of the faces. Participants were instructed to maintain fixation and to indicate for each stimulus whether it was a face or ''nonface,'' using the right middle or index finger (counterbalanced between subjects). Note that we did not impose person-discrimination judgments during scanning, because we sought to avoid the fMRI results from potentially being confounded by performance or ''task difficulty''. Approximately 30% null events of 3-sec length with a fixation point were further added to jitter the events and allow the signal to saturate, hence optimizing the estimated response (Friston, Zarahn, Josephs, Henson, & Dale, 1999). The order of trials was pseudorandomized to maximize the separation in time between repeating faces with the same features or with the same second-order spatial relations. Each pair was presented three times in three different consecutive fMRI sessions. Each fMRI session was divided into two epochs, separated by a 5-sec break in which participants got feedback regarding their reaction times and accuracy in discriminating nonfaces from faces. Thirteen of the fMRI participants performed the person-discrimination experiment (as in Experiment 1) immediately after scanning. The procedure was identical except that the image size was larger (19.5 cm^2), and correspondingly, the viewing angle wider ($\sim$21.3°). Note as well that for the second cohort as opposed to the unscanned, the stimuli set was familiar, because they have seen each face at least thrice before making the person-discrimination task. Thirteen participants also gave a subjective rating of their face-recognition skill in daily life (as in Experiment 2c) after the experimental session ended.

Scanning

A Siemens 1.5-T Sonata system (Siemens, Erlangen, Germany) was used to acquire blood oxygenation level-dependent gradient echo-planar images (EPI). Images were reconstructed using trajectory-based reconstruction (TBR) to minimize ghosting and distortion effects in the images (Josephs, Deichmann, & Turner, 2000). Thirty-two oblique axial slices (2 mm thick with 1.5-mm gap) were acquired with 64×64 pixels and in-plane resolution of 3×3 mm^2, 90° of flip angle, 30 msec of echo time, and 2880 sec of repeat time. To reduce susceptibility artifacts in the anterior and posterior temporal cortices, slices were tilted 30° anteriorly (Deichmann, Gottfried, Hutton, & Turner, 2003). Subsequent to the functional scans, a T1-weighted structural image ($1 \times 1 \times 1$-mm resolution) was acquired for coregistration and for anatomical localization of the functional results.

Data Analysis

Whole-brain voxel-based analyses were performed with SPM2 (www.fil.ion.ucl.ac.uk/spm/). EPI volumes were realigned and unwarped to correct for artifacts due to head movements (Ashburner & Friston, 2003a; Andersson, Hutton, Ashburner, Turner, & Friston, 2001). The time series for each voxel was realigned temporally to the acquisition of the middle slice. The EPI images were normalized to a standard EPI template, corresponding to the MNI reference brain and resampled to $3 \times 3 \times 3$-mm voxels (Ashburner & Friston, 2003b). The normalized images were smoothed with an isotropic 9-mm full width half maximum Gaussian kernel, in accord with the SPM approach.

Statistical analysis in SPM2 uses summary statistics with two levels (Kiebel & Holmes, 2003; Penny, Holmes, & Friston, 2003). At the first level, single-subject fMRI responses were modeled by a design matrix with regressors for each condition, depicting the onset of the second face in a pair. The onset regressors were convolved with the canonical hemodynamic response function (Friston, Glaser, Mechelli, Turner, & Price, 2003). Effects of no interest were also modeled, including regressors for the onsets of feedback events, the onset of the first face in each pair regardless of the subsequent stimulus, the scanning sessions, and harmonics that capture low frequency changes of the signal to account for biological and scanner noise (equivalent to high-pass filtering of the data at 1/128 Hz). Note that in this design, the critical conditions differed only in respect to how the second face related to the first face in a pair, with the latter held constant across conditions and counterbalanced across subjects (Figure 1A). Accordingly, only the critical SPM results for the four regressors relating to the second face in each successive pair are reported. Linear contrasts pertaining to the main effects, interactions, and simple effects were calculated for each subject. To allow inferences at the population level, a second-level random-effects analysis was performed, where subjects were treated as random variables. Here, images resulting from contrasts calculated for each subject were entered into a new analysis and tested for significance using a one-sample t test. Figure 3 presents the resulting SPM Student's t maps threshold at $p < .005$ (uncorrected). We present only results that were consistent across subjects (i.e., in the random-effects group analysis).

Correlations of behavioral outcomes (e.g., impact of second-order spatial relations and of features on person-discrimination performed outside the scanner, calculated for individual participants just as for Experiment 1) with blood oxygenation level-dependent response were tested using linear correlation (Pearson) analysis across subjects as implemented in SPM2. A whole-brain analysis tested for correlations between the behavioral and contrast images that measure effects of the same type of information within faces. Specifically, given the above behavioral results (Experiment 2), we tested for any correlation between the behavioral impact of second-order spatial relations and the size of the fMRI effect for second-order spatial relations change minus repeat for each individual participant. An analogous procedure was

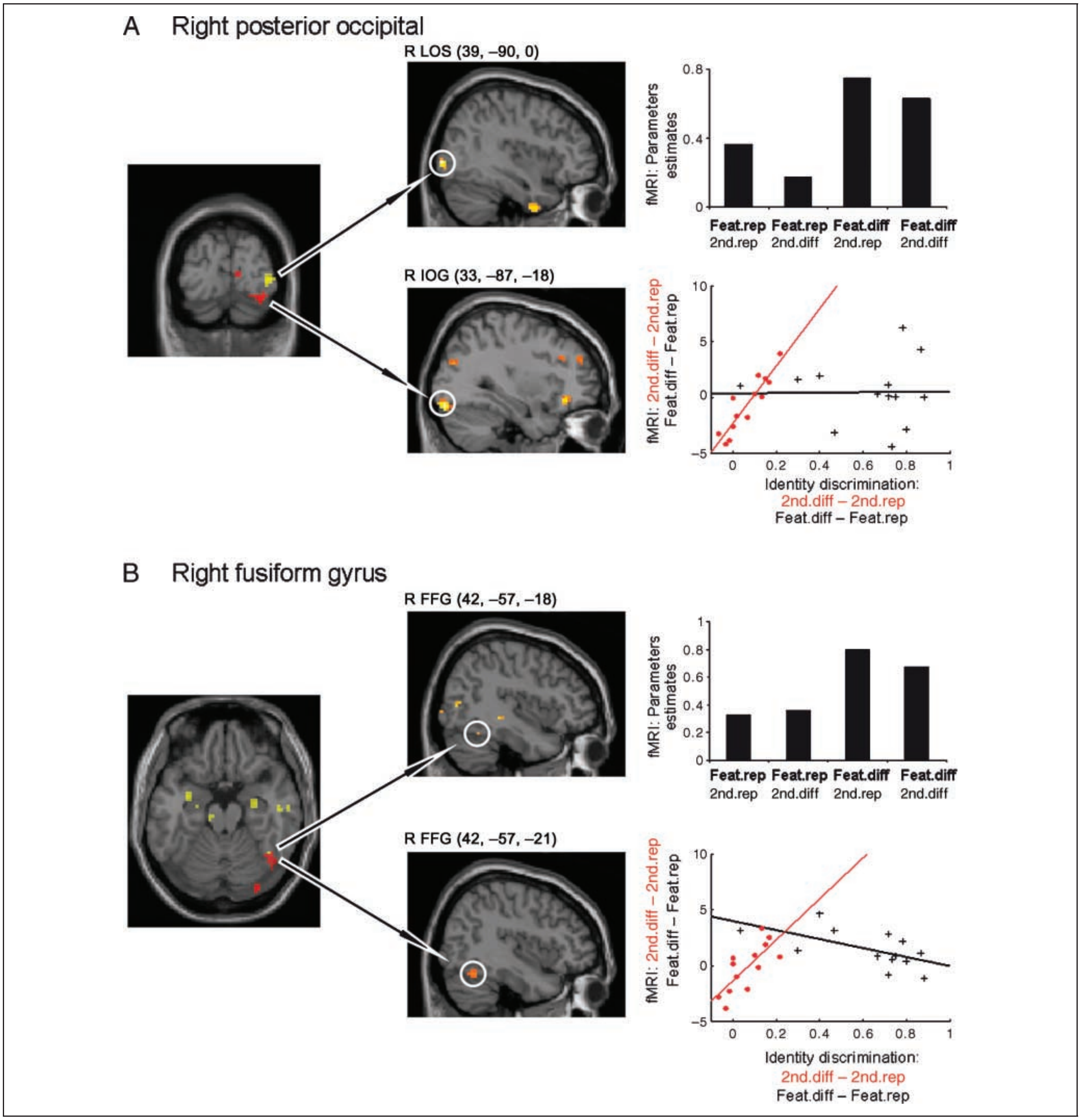

Figure 3. fMRI experiment results. On the left, two overlaid SPM maps (yellow and red) are presented on a T1 template image of a single subject. Yellow = areas showing significant main effects of featural changes; red = areas showing significant correlations of brain responses to second-order spatial relational change with the impact of such changes on individual participants' behavioral person discriminations, measured in a separate behavioral study (see main text). In the middle column, the corresponding SPMs are overlaid on a sagittal T1 template image, depicting each effect separately. For presentation purposes, all SPM map thresholds are $p < .005$. In the right columns, plots of parameters estimates taken from the maxima (MNI coordinates given in central column) are plotted for each of the four experimental conditions, and scatterplots are shown for the effects of second-order spatial relation changes on fMRI activity (coordinates above) against the behavioral impact of such changes on person discrimination (see red dots). For comparison, responses in relation to the behavioral impact of featural change on the fMRI response to featural change (no correlation found) are also plotted for the same maxima (black pluses). (A) Separate featural and second-order spatial relation effects in posterior occipital cortices (LOS and IOG, respectively). (B) Convergence of featural and second-order spatial relation effects (latter related to individual differences in behavioral impact of relational changes) in the right FFG. 2nd.diff = changes of second-order relations; 2nd.rep = repetition of second-order relations; Feat = feature.

used to test for any correlations between the individual behavioral impact of feature changes and the fMRI effect of feature changes minus repeat; and between the subjective reports of face-recognition skill and brain responses to changes in features or in second-order spatial relations. The correlation scatterplots (Figure 3) plot the parameter estimate measures for each participant taken from the maxima within the occipito-temporal cortex where bold signal for second-order spatial relations changes correlated with their measured behavioral impact. For comparison and to test for subthreshold effects, the parameter estimates for the feature change from the same maxima (as above) are also plotted against the behavioral impact of featural change for each participant. Significance was tested using two-tailed t tests with $n - 2$ degrees of freedom.

Analyses of the behavioral experiments (the person-discrimination task and the subjective rating of face-recognition skill) were implemented with the same statistical tests as in Experiments 1 and 2c.

Functional Localizer of Face-preferential Voxels

To assess whether any of the fMRI effects observed in the main 2 × 2 experiment overlapped with voxels that may show preferential activation to faces versus other classes of objects, we implemented a separate functional localizer scan for 13 of our 14 participants. Stimuli for this localizer included 20 achromatic close-up photos of unfamiliar faces (Henson et al., 2003), cropped with an ellipse to exclude outer contours, plus 20 achromatic photos of houses cropped with an ellipse to match the same outline frame as the faces. In addition, scrambled versions of the faces were generated, initially, in a checkerboard grid of 13 × 10, which was then cropped by the same ellipse outlines as the faces. Stimuli for the functional localizer were presented in a blocked design, with 20 stimuli from the same category in each block (faces, houses, or scrambled faces). The blocks of 20-sec duration were separated with a 10-sec fixation point presented on a gray background. Each stimulus was presented for 500 msec, with an interstimulus interval of 1000 msec, during which a fixation cross on a gray background was presented. The participants' task during the localizer blocks was simply to detect any immediate repetition by a button press, which occurred approximately 15% of the times equally distributed across all blocked conditions. Each block was repeated twice or thrice.

The localizer fMRI data were acquired using an identical magnetic resonance sequence and protocol as above and were preprocessed in the same manner. For each subject, face-preferential voxels were then delineated using the contrast [faces − (houses + scrambled faces)]. A second-level analysis then tested for consistent localization of face-preferential voxels across subjects using a one-sample t test. The outcome of this comparison was used as an inclusive mask (with the conventional threshold for masking of $p < .05$ uncorrected) within SPM2 to test whether any of the fMRI effects reported in the main experiment (i.e., changes of features and/or of second-order spatial relations within faces) overlapped with face-preferential voxels.

Results

Participants in the fMRI experiment performed the person-discrimination task (as in Experiment 1) and gave subjective self-rated face-recognition skill (as in Experiment 2c) after the fMRI session. The results of these two new behavioral data sets replicated the results reported in Experiment 1 and 2c. The new results for person discrimination did not differ from those of Experiment 1 tested using a mixed design analysis of variance with scanned unscanned participant as a between-subject factor and change/repeat featural or second-order spatial relations as within factors, for any terms [all the interactions with the cohort factors were $F(1,29) < 1, p > .3$]. We next describe the results of the analysis of only the second cohort. As in Experiment 1, participants were more likely to judge two faces as reflecting two different people when features changed compared with when they repeated [$F(1,12) = 80.2, p < .001$], and likewise, albeit to a lesser extent, when second-order spatial relations changed compared with repeated [$F(1,12) = 7.1, p < .05$]. As in Experiment 1, the impact of feature changes on proportion of "different" responses (0.61 ± 0.2) was much larger than the impact of second-order spatial relation changes [0.065 ± 0.08; $t(12) = 7.85$, $p < .001$] and these two impacts did not correlate [Spearman's $\rho = -0.088$, $t(11) = 2.88$, $p = .3$]. Here, changes in spatial relations led to more frequent reports of a different person when features repeated than when features changed [$F(1,12) = 7.8, p < .05$].

Importantly, the relation between person discrimination and subjective self-ratings of recognition skill in the new behavioral data set also replicated Experiment 2c. Again, only the impact of second-order spatial relation changes related to participants' face-recognition skill [Spearman's $\rho = 0.674$, $t(10) = 2.88$, $p < .05$] not the impact of feature change [Spearman's $\rho = -0.004$, $t(10) = 0.293$, $p = .91$]. Taken together, the new behavioral results from the scanned participants replicate the findings for the earlier behavioral tests. Person-discrimination judgments were more influenced by featural than by second-order spatial relation changes, although the latter also contributed significantly. The impact of second-order spatial relations (on proportion of "different" response) for individual participants again correlated with self-rated face-recognition skill, but the individual impact of feature changes did not.

During scanning, participants had to monitor each stimulus to determine whether it was a face or a nonface (see Methods). This monitoring task was implemented to avoid confounding repetition-related effects with response requirements (Henson, Shallice, Gorno-Tempini, & Dolan, 2002). Mean accuracy to detect faces from nonfaces was 90%, and this was not affected by whether the preceding face in the stream had same or different features or the same or different second-order spatial relations (all *p*s > .1). Furthermore, participants' performances on the face/nonface task were not affected by the impact of features or second-order spatial relation measured above (all *p*s > .1). Mean latency to respond to the face stimuli was 505 msec, and this was unaffected by our experimental conditions (all *p*s > .2). This confirms that any effects measured by the fMRI cannot be attributed to differences in task difficulty between the different conditions, thereby making attentional or strategic differences between conditions unlikely also, given the constant face/nonface task with equivalent performance.

Given the findings from previous neuroimaging studies on face processing and, in particular, on putative configural and featural aspects (Yovel & Kanwisher, 2004; Lerner et al., 2001; Rossion et al., 2000), we focus primarily on fMRI effects found within occipito-temporal cortices. But for completeness, Table 1 lists all regions anywhere in the brain surviving $p < .001$ (uncorrected) that involved more than 10 contiguous voxels. There was no reliable interaction between changes to features and second-order relations in any brain area. Thus, we report and discuss main effects and correlations only.

fMRI effects due to featural change were assessed by contrasting conditions in which the features were repeated versus changed, irrespective of second-order spatial relation conditions (i.e., main effect of featural change minus featural repetition). The bilateral LOS and the right FFG (Figure 3 and Table 1A) showed relatively higher activation when features were changed versus repeated within successive pairs of face stimuli in the stream. Clusters within bilateral LOS and the right FFG overlapped with face-preferential voxels as identified by the separate functional localizer, suggesting these regions may have more involvement in processing faces than other object types (Table 1A and Methods).

Possible fMRI effects due to second-order spatial relation changes (initially disregarding individual differences in the impact of such change) were assessed by comparing conditions in which second-order spatial relations changes versus repeated, irrespective of featural conditions (i.e., main effect of spatial relation changes minus spatial relation repetition). Only the right intraparietal sulcus (Table 1B), outside of the occipito-temporal visual cortex, showed significant increases in response when second-order spatial relations changed (compared with repeating). This activation might potentially be related to the role of right parietal cortex in more global or configural processing (cf. Fink et al., 1996; Robertson, Lamb, & Knight, 1988), because changes of second-order spatial relations may affect global processing more than changes of featural information in faces (Farah et al., 1998). However, given our a priori interests in the occipito-temporal cortex, we do not speculate further on this.

Table 1. Consistent fMRI Results across Subjects

Anatomical Location	*H*	*Z*	*MNI*		
			x	*y*	*z*
A. Main effect of feature change: features differed − features repeated					
LOS	R	4.15	39	−90	0
		3.07	45	−75	9[a]
	L	2.76*	−42	−60	3[a]
FFG	R	2.63*	42	−54	−21[a]
Amyg	R	3.22	30	−9	−21[a]
	L	3.47	−30	−6	−27[a]
B. Main effect of second-order configural relations change: 2nd.diff > 2nd.rep					
IPS	R	4.15	48	−39	36
C. Correlation of behavior and fMRI: second-order configural relations					
IOG	R	4.31	33	−87	−18
	L	3.85	−45	−75	−12
		2.80*	−45	−81	−6[a]
FFG	R	2.93*	42	−57	−21
		2.66*	45	−54	−21[a]
IFG	L	4.54	−33	36	24
SFG	R	4.11	18	63	12
	L	3.47	−18	18	42
CG		3.57	−3	−9	36
IFG/insula	R	3.75	33	33	−12
Putamen	L	3.39	−24	−3	9

OFC = orbital frontal cortex; aSTS = anterior superior temporal sulcus; MTS = middle temporal sulcus; Amyg = amygdala; CG = cingulate gyrus; aHipp = anterior hippocampus; IPS = intraparietal sulcus; IFG = inferior frontal gyrus; SFG = superior frontal gyrus; H = hemisphere; L = left; R = right; 2nd.diff = changes of second-order relations; 2nd.rep = repetition of second-order relations.

Statistical significance of peak activation, two-tailed tests: all $Z > 2.98$, $p \leq .002$, aside from $^{*}p < .008$.

[a] Peak that overlaps with face-preferential voxels across subjects (tested using inclusive mask $p < .05$, uncorrected).

When disregarding individual differences, there were no reliable fMRI effects for changes of second-order spatial relations in the occipito-temporal cortex. But when considering individual difference in the behavioral impact of second-order relational changes (which had been found to be crucial in the preceding behavioral experiments), some clear fMRI results were found. We analyzed the fMRI data to assess differential effects that depended on the interparticipant impact of second-order relational changes, as assessed (for $n = 13$) in the behavioral session of the person-discrimination task after scanning. Specifically, we tested for correlations between the individual impacts of second-order spatial relation changes on behavioral person discrimination (outside the scanner), with brain responses to such stimulus changes, for each individual, inside the scanner during the monitoring (face/nonface) task. We also tested any analogous brain-behavioral relations for the impact of featural changes. Reliable brain-behavior correlations were found only for the second-order spatial relation changes. The individual behavioral impact of second-order spatial relation change (measured subsequent to scanning) correlated positively with increased activity due to second-order spatial relation changes (minus repeats) in the bilateral IOG and in the right FFG (see Figure 3 and Table 1C). Note that these neural effects critically depended on the impact of second-order spatial relation changes on each participant, as assessed with a separate behavioral measure, because there was no overall main effect for second-order relations changes in these regions when disregarding individual differences (see above).

Moreover, by using the separate functional localizer data to delineate face-preferential voxels, we show that part of the left IOG and the right FFG clusters overlapped with face-preferential voxels (Table 1C), indicating that these regions may engage more in face processing than for other types of objects. No brain region showed a featural change effect that correlated with individual differences in the (separately measured) behavioral impact of feature changes.

Turning to subjective self-ratings of face-recognition skill, remarkably, we found that these also positively correlated with the effect of second-order spatial relational change for each participant in the left IOG [−42, −84, −3: Pearson $r = .76$, $t(11) = 3.89$, $p = .002$]. This raises the intriguing possibility that recruitment of these regions for encoding of changes in second-order relations may be associated with improved face-recognition skill.

Recall that in the behavioral results, subjective rating of recognition skill did not correlate with the impact of featural change. Likewise, there was no correlation of such subjective ratings with the subject-by-subject fMRI impact of featural changes, unlike the positive relationship found for second-order spatial relation changes in the IOG.

Taken together, these fMRI data suggest that, in posterior occipital regions, featural and second-order relational aspects of faces may be processed separately (Figure 3), albeit with an important role for individual differences in sensitivity to second-order spatial relation changes. Responses of the right LOS were affected by a change of features [$t(13) = 6.18$, $p < .001$] but not by second-order spatial relations changes [$t(13) = -1.4$, $p = .2$] and were unrelated to the impact of second-order spatial relations changes for particular individuals [Pearson $r = .05$, $t(11) = 0.16$, $p = .8$]. Conversely, bilateral IOG effects of second-order relational changes were reliably correlated (see above) with separately measured behavioral impact of relational change for each individual subject. Yet, IOG was unaffected by featural change overall [right IOG: $t(13) = 0.5$, $p = .3$; left IOG: $t(13) = 0.7$, $p = .2$] and showed no reliable positive correlation with the individual behavioral impact of features [right IOG: $t(13) = 0.074$, left IOG: $t(13) = -0.5$; see Figure 3]. It may be noteworthy that the functionally dissociated brain responses for featural or second-order spatial relation changes were observed in relatively posterior regions of the occipital cortex. Previous studies have reported face-preferential voxels in posterior occipital cortices (Hasson, Harel, Levy, & Malach, 2003; Levy, Hasson, Avidan, Hendler, & Malach, 2001; Kanwisher, McDermott, & Chun, 1997), as also observed here. One concern relates to the possibility that our effects were driven solely by low-level visual changes between the face pairs. However, we note that both the second-order spatial relations and featural changes were small in terms of degrees of viewing angle (<1°) and that the affected regions fell primarily anterior to retinotopic visual areas, rather than arising in the very earliest regions such as the calcarine sulcus. Hence, it seems unlikely that these effects reflect retinotopic factors per se.

The right FFG (peak MNI: 42, −54, −21) showed two critical effects. It was affected by featural change [$t(13) = 3.1$, $p < .005$] but also showed a second-order spatial relations influence that was related to the individual impact of relational changes on individuals' person-discrimination behavior [Pearson $r = .7$, $t(11) = 3.25$, $p < .005$]. These two results indicate that, unlike more posterior regions, the right FFG may be involved in both featural and in (individually varying) second-order relational processing, with these two types of information potentially converging here. Note also that the right FFG cluster overlapped with face-preferential voxels.

GENERAL DISCUSSION

In a series of behavioral experiments and an fMRI experiment, we studied the role and impact of featural face information (eyes, nose, and mouth regions) and of second-order spatial relations among these same features (Maurer et al., 2002). Unlike recent studies (Yovel & Kanwisher, 2004; Le Grand et al., 2001) that sought to "match" the discrimination difficulty of featural and second-order spatial information using artificial ranges, we took the alternative approach of manipulating our stimuli according to the ranges within the different photos of real natural faces. Hence, variability in eyes, nose, and mouth features and, likewise, the variability in the second-order spatial relations of these features matched the variability of the original real faces in these operationally defined aspects.

In an on-line person-discrimination task (Experiment 1), we found that changes in the features had a bigger overall influence on the proportion of ''different-person'' responses and that second-order spatial relations changes also had some impact, with these influences varying from one participant to another. Experiments 2a–2c applied three very different measures of face-recognition ability to participants from Experiment 1. Experiment 2a assessed incidental learning of new faces, as tested by yes/no recognition after delays of approximately 45 min (and more than 250 intervening face stimuli). Experiment 2b assessed familiarity judgments for famous faces intermingled with unknown faces. Experiment 2c obtained ratings of participants' estimates of their own face-recognition skill in daily life. Thus, although Experiments 2a and 2b used objective measures of recognition sensitivity (d'), Experiment 2c provided a purely subjective self-rating.

Remarkably, we found that the behavioral impact of second-order spatial relational changes on person discrimination in Experiment 1, for each participant who also underwent Experiment 2, correlated positively with the three separate measures of face recognition (see Figure 2D–F dots in top row of scatterplots). This provides an entirely new line of evidence, from individual differences among neurologically intact participants to a role of second-order relational processing in face-recognition skills. The impact of second-order spatial relations on each participant's person discriminations in Experiment 1 did not correlate with the impact of featural changes. Moreover, the latter showed no relation to incidental learning of new faces or to subjective ratings of face-recognition skill, although it did show some correlation with familiarity judgments for famous faces (indicating that high impact of features may become an advantage for overlearned individuals, in addition to second-order spatial relations).

Turning to our fMRI data (Experiment 3), participants now solely had to monitor the face stimuli (for nonface deviants), while we varied whether features and/or second-order spatial relations repeated or changed. Featural change (vs. repetition) led to reliable activation in the bilateral LOS and in the right FFG, with part of these clusters overlapping with face-preferential voxels, as determined from a separate functional localizer. These results may accord with recent reports suggesting that facial features are processed in the LOC (Yovel & Kanwisher, 2004; Lerner et al., 2001). Note that LOC is a functionally defined region that typically includes the lateral and ventral banks of the occipital cortex (Malach, Levy, & Hasson, 2002). LOC is hypothesized to be a complex of several subregions with subparts preferentially responsive to faces (Malach et al., 2002). Our results suggest that LOC subdivisions may reflect processing demands, namely, featural versus second-order spatial relations, and not just stimulus category (Malach et al., 2002). Our data suggest that these two processing types overlapped for some clusters with face-preferential voxels but may not always be specific to faces (as shown by Yovel & Kanwisher, 2004; Lerner et al., 2001).

In accord with a recent study that reported no overall changes in activation for second-order spatial relations versus featural properties (Yovel & Kanwisher, 2004), here, we likewise found no overall effect of second-order spatial relational change versus repetition when ignoring individual differences. However, when taking into account individual differences in the impact of second-order spatial relations changes on person discrimination (as assessed in the separate behavioral session), we found that the bilateral IOG (and also the right FFG) showed activations for second-order spatial relations change that correlated with the individual participants' behavioral impact of such changes. This outcome suggests that neurologically intact individuals vary in the extent to which they rely on second-order spatial relations information from faces when discriminating people. Moreover, here we found that this variation can be reflected in their brain responses when monitoring faces. Furthermore, we also found rather remarkably that this fMRI effect correlated with self-ratings of face-recognition skill in daily life for the IOG.

The present study points to the importance of considering individual differences in face processing among the normal population. We found that the behavioral impact of second-order relational changes varied between individuals in a way that related to three separate measures of face-recognition skill (incidental learning of new faces, familiarity judgments for famous faces, and self-ratings of face-recognition skill in daily life). Moreover, variation in the behavioral impact of second-order relational changes also related to brain activations for such changes in the bilateral IOG and in the right FFG. It may be worth noting that within these peaks of correlation, some participants showed increased activation when spatial relations were repeated compared with when they were changed (i.e., an inverse of the usual repetition-decrease phenomenon). Increased fMRI responses after face repetitions in the occipito-temporal cortex have been observed by some other studies (e.g., Henson & Rugg, 2003; George et al., 1999). Furthermore, it has been suggested that stimulus repetition may lead to fMRI increases or decreases, depending on expertise and initial processing difficulty (Kourtzi, Betts, Sarkheil, & Welchman, 2005). Decreases after stimulus repetition may occur if processing is easy (e.g., with salient stimuli), whereas increases may occur if the task is difficult and performance is initially poor (Kourtzi et al., 2005). This perspective may fit nicely with our results, because, here, repetition of second-order spatial relations led to a localized fMRI increase for those subjects that were relatively poor at processing spatial relational changes within faces (as shown by the small impact of such changes on their person discrimination), unlike subjects who were relatively good at processing this stimulus dimension (as shown by the larger impact for them). It may be interesting to test in future research whether supervised learning could invert the fMRI repetition effect of second-order spatial relations within faces for the less ''expert'' participants.

Our results may relate to previous findings emphasizing the role of second-order spatial relational processing (more than featural processing) in face-processing deficits such as prosopagnosia (Barton et al., 2003; Joubert et al., 2003; Saumier et al., 2001; de Gelder & Rouw, 2000a; Farah, Wilson, Drain, & Tanaka, 1995). Although the classic literature on prosopagnosia dealt with neurological patients, there has been increasing interest in the possibility that prosopagnosic-like deficits may exist within the otherwise ''normal'' population, reflecting a developmental disorder (Duchaine & Nakayama, 2006; Behrmann & Avidan, 2005; Barton et al., 2003). None of our present participants reported face deficits in daily life, and none was within an abnormal range for recognizing famous or recently exposed faces (see Experiment 2). Nevertheless, our results indicate that processing of second-order spatial relations and face recognition may be related skills that vary within the ''normal'' population. Indeed, none of the most critical findings here (i.e., the correlations between different behavioral measures or between a behavioral measure and an fMRI outcome) could have been obtained without considering individual differences. Identifying the causes of these individual differences (which might be genetic, experience-dependent, or both) requires future research. This may also address whether individuals with congenital or developmental prosopagnosia simply fall at one extreme end of a face-processing skill continuum or instead differ qualitatively from normal variation in sensitivity to second-order spatial relations (see Duchaine & Nakayama, 2006; Behrmann & Avidan, 2005).

Individual differences in the impact of featural changes, rather than second-order spatial relations, did not correlate with any other measure here, with the exception of familiarity judgments for famous faces. It may be that features do eventually become recognizable in overlearned faces. This accords with anecdotal reports that prosopagnosic patients occasionally recognize faces by relying on distinctive facial features (Bentin, Deouell, & Soroker, 1999). Other prosopagnosic patients may show deficits in featural and not just second-order relational processing (Yovel & Duchaine, 2006). The in-principle sufficiency of well-learned featural processing for recognition of highly familiar faces accords with evidence from machine learning, where successful algorithms often rely on featural rather than second-order spatial relation information (Hancock, Bruce, & Burton, 1998). Recognition performance with such approaches typically depends closely on the number of face exemplars the system has received for a particular individual during training (Burton, Jenkins, Hancock, & White, 2005). However, we found here that interparticipant differences in the impact of second-order relations showed stronger links to recognition performance (and to brain activity in IOG and FFG) than did individual differences in the impact of featural changes.

It has been argued theoretically that encoding of both features and their second-order configural relations might be explained in one step, by a simple shape-based model (Jiang et al., 2006; Riesenhuber, Jarudi, Gilad, & Sinha, 2004). We showed that the behavioral impacts of featural or second-order spatial relations changes did not correlate across participants and that different brain areas were implicated in their processing (once individual differences were taken into account). Featural (but not second-order relational) changes were associated with activity in LOS responses, whereas second-order changes (in relation to their behavioral impact for each participant) were associated with IOG responses, but featural changes were not. Our behavioral and fMRI findings provide a new line of support for the idea that both featural processing and second-order spatial relational processing make distinct contributions to face processing (Jiang et al., 2006; Yovel & Duchaine, 2006; Farah et al., 1998; Sergent, 1984). They seem less consistent with strongly ''holistic'' approaches to faces, which might argue that features and their second-order relations are interdependent aspects of faces that cannot be separated (see Yovel & Duchaine, 2006; Tanaka & Sengco, 1997; Rhodes, 1988).

Finally, the pattern observed here for the right FFG suggest that it is a region where featural and second-order relational information converge. We found not only an overall increase in activity for featural changes but also an effect of second-order configural changes that related to the behavioral impact of such changes for each participant. These new findings for the FFG are in line with recently proposed hierarchical models for face discrimination (Jiang et al., 2006; Riesenhuber et al., 2004), which suggest that information from lower computational levels (e.g., posterior occipital cortices), where neural populations encode separable aspects of faces (e.g., featural vs. spatial relational) project to more anterior regions along the ventral stream, where the two types of information converge to establish a representation of a unique identity.

In conclusion, our new behavioral results indicate that although facial features have a prominent role in person discrimination (and to some extent, in recognition of overlearned famous faces), second-order spatial relations are important for face recognition. Individual differences in the impact of these configural relations correlated with variation in objectively assessed face recognition (for both newly learned and famous faces) and also with subjective self-ratings of face-recognition skill in daily life. Finally, it will be important in future fMRI work to take individual differences within the normal population into account, because this was critical here for revealing effects of configural second-order spatial relations on the bilateral IOG and right FFG.

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